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SEEDLING ANATOMY OF CYNARA
SCOLYMUS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

1935

By
WALTER SARGEANT PHILLIPS

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SEEDLING ANATOMY OF CYNARA SCOLYMUS
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 479

WALTER S. PHILLIPS

(WITH TWENTY-TWO FIGURES)

Introduction

According to DE CANDOLLE (2) *Cynara scolymus* L., the Globe artichoke, is a native of the Mediterranean region. MORIS, DE CANDOLLE reports, cultivated *C. cardunculus* and *C. scolymus* side by side and found no true specific distinctions. He therefore applied the name *C. cardunculus* var. *sativa* to *C. scolymus*. STURTEVANT (14) discussed the synonymy and history of this species. At the present time the most important area for commercial production in the United States is along the California coast, between Santa Barbara and San Francisco, where about 9000 acres are devoted to its cultivation (11).

Little morphological work has been done with *Cynara scolymus*, and this has dealt chiefly with the chemical contents of the flower heads, which constitute the commercial part of the plant. OKEY and WILLIAMS (9) reported inulin as the chief carbohydrate, with a small percentage of reducing sugars also present. SCOTT (11) discussed propagation briefly and also included chemical analyses of the subterranean and aerial parts of the plant. LE FEUVRE (8) and WELLINGTON (19) investigated propagation and cultivation. JEFFREY (6) considered the tribe Cynareae as "transitional anatomically from the Tubuliflorae to the Liguliflorae," and regarded the oil canals found in *C. scolymus* as primitive structures in what he considered to be the more stable parts of the plant. SACHS (10) and VAN TIEGHEM (18) described the oil canals or ducts, which are of schizogenous origin and occur between the two layers of the endodermis. These have been reported as occurring in many members of this family, according to SOLEREDER (13).

Material and methods

The seeds used in this investigation were obtained from the Bureau of Foreign Plant Introduction at their Chico, California, sta-

tion, and also from a commercial seed company. Three varieties, Green Globe, Flat Brittany, and Large Globe or Paris Improved, were found to be practically identical in their seedling anatomy. The straightest seedlings were grown on moist paper in tumblers, but in order to check their development with seedlings grown in soil, akenes were also planted in soil and serial sections of these plants were compared with those germinated on paper. No morphological differences were found.

Navashin's solution and chrom-acetic solutions proved the best fixatives. After fixing, the material was washed for several hours in warm water to soften and dissolve the inulin as much as possible. Serial sections were cut 8-15 μ in thickness and stained with Flemming's triple stain or with safranin and fast green. The safranin-fast green stain was very satisfactory in making drawings with microprojection apparatus.

Investigation

Cynara scolymus is propagated by suckers or by seed. The sucker method is usually followed because it brings the plants into commercial production sooner. The plant is a perennial with the rosette habit, the flower stalk not appearing until the second year in plants grown from seed. As soon as the flower stalk dies back, about a dozen new shoots develop from axillary buds of the rosette leaves. SCOTT reports that these new shoots develop an adventitious root system and that the old primary root becomes fleshy and functions as a storage organ.

The fruit is an akene containing a single erect anatropous ovule. Endosperm is lacking and the nucellar tissue consists of a thin membranaceous layer of cells closely adhering to the ovary wall. The small hypocotyl and epicotyl lie at the basal end of the ovary, and the two thick cotyledons fill the remainder.

At germination the primary root pushes through the coats of the akene by the second or third day. Rapid elongation of the primary root takes place first; then the hypocotyl elongates and raises the cotyledons, partially inclosed in the akene, above the ground. The cotyledons expand rapidly and function as fleshy photosynthetic

leaves for several days before the first epicotyledonary leaves appear. The mature cotyledons are obovate, tapering slightly toward the thick fleshy petioles.

PRIMARY ROOT

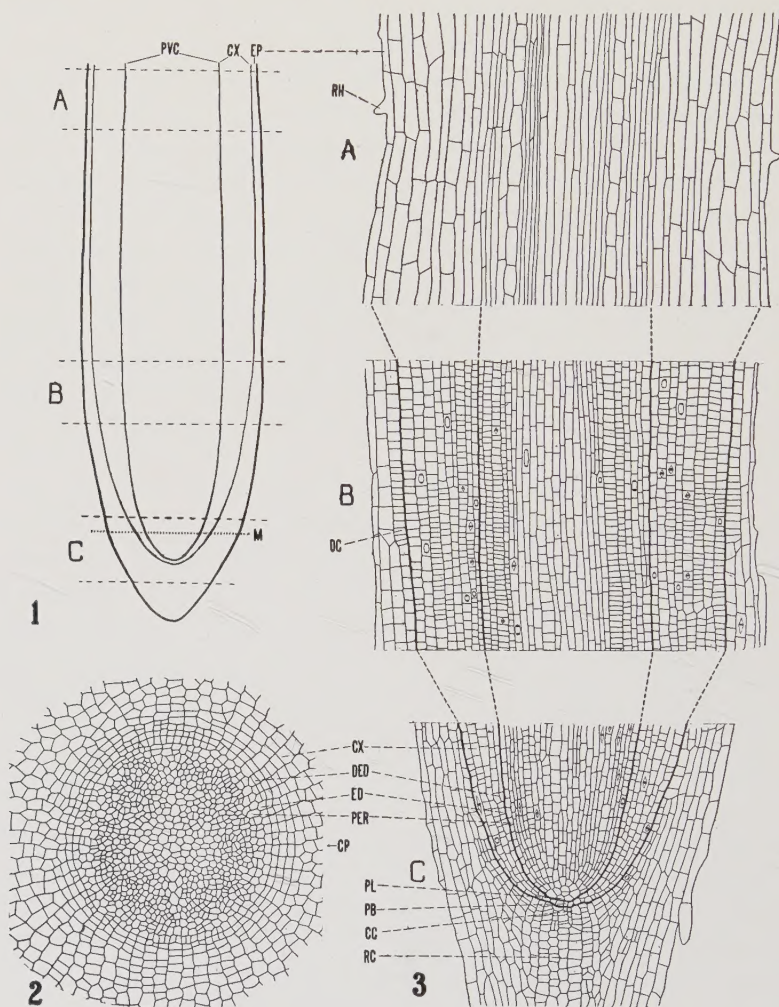
The primary root is diarch, with the four or five protoxylem elements of each point alternating with two lateral bands of phloem cells. JEFFREY (6) has figured the primary root as triarch, but in the seedlings examined this condition was never encountered. Some of the adventitious roots of older plants were tetrarch. Parenchymatous cells separate the phloem from the xylem in the region where the cambium is later to develop, and there are several large parenchymatous cells in the central region of the stele. This whole cylinder of vascular tissue is surrounded by the pericycle, which is at first uniseriate. The primary xylem elements remain intact after secondary thickening has taken place, and are clearly discernible in the mature root.

The endodermis limits the cortex centripetally, but Casparian strips are not developed until after there has been some secondary thickening. The endodermis can be distinguished from the other cortical cells by the early development of primary endodermal oil ducts, which accurately locate the endodermal layers even before the formation of the Casparian strips. The layers of cortical cells adjacent to the endodermis have a radial arrangement which is lost in the outer limits of the cortex. The cortex persists intact for a considerable time, but after secondary thickening of the axis has started, a phellogen is formed midway between the endodermis and the epidermis and the outer cortical cells and epidermis slough off.

The development of the primary root axis is similar to that described by JANCZEWSKI (5) for *Helianthus annuus*. It follows his third type, in which plerome and periblem produce stele and cortex respectively and a common layer initiates both the epidermis and calyptra.

This common layer of cells overlying the periblem has been termed the calyptragen-dermatogen by CROOKS (3) because both the root cap and the epidermis are derived from it. ERIKSSON (4) has referred to it as the dermacalyptragen. This layer divides in a series of periclinal divisions at the apex of the root, giving rise to the more

or less radially arranged cells of the terminal portion of the root cap (figs. 1, 3C). Periclinal divisions also occur in the lateral por-



FIGS. 1-3.—Fig. 1, diagrammatic representation of root tip. A, B, and C represent areas shown in detail in fig. 3. M, position of cross section shown in fig. 2. Fig. 2, cross section through meristem of root at level where endodermal layer divides. Fig. 3, A, B, C, longitudinal sections of root. *cg*, calyptrogen; *cp*, cotyledonary plane; *cx*, cortex; *ded*, double endodermis; *dg*, dermatogen; *ed*, single endodermal layer; *ep*, epidermis; *pb*, periblem; *per*, pericycle; *pl*, plerome; *rc*, root cap; *rh*, root hair.

tions of this layer, where anticlinal divisions are taking place. In this manner the root cap becomes an elongate structure extending some distance upward from the tip of the root, but being thickest at the apex. The lateral portions of this layer form the epidermis by a series of anticlinal divisions (fig. 3*B*).

The cortex is derived from a single layer of cells, the periblem, which lies directly inside the calyptrogen-dermatogen layer. The endodermis, which limits the cortex on the inside, is a cylindrical layer of tissue two cells in thickness, with structural features unlike those of the cells on either side. This double layer of cells originates from the innermost layer of the periblem near the apex of the root by a single periclinal division (figs. 2, 3*C*). The cytoplasm in the endodermal cells is dense and contains no inulin crystals. Oil ducts develop by the formation of schizogenous intercellular spaces between these two layers of endodermal cells. These are not formed where the endodermis lies exterior to the protoxylem points. BARY (1) considers corresponding cell layers in other plants as endodermal but in this case only the layer next to the stele has been found to develop Casparian strips. These ducts have been described by SACHS (10) and VAN TIEGHEM (18). SOLEREDER (13) summarizes the work on oil ducts done in this and other groups of plants.

The plerome gives rise to the stele and consists of a small group of cells directly within the periblem. The larger parenchymatous cells at the center of the axis are discernible at an early stage in the differentiation of the stele. The pericycle, which is at first a single layer, becomes several cells thick by means of tangential divisions of its cells (fig. 21). The first vascular tissue to differentiate is the primary phloem, which is formed by divisions in a vertical plane of the plerome cells immediately within the pericycle. Six primary phloem ducts, three on either side of the cotyledonary plane, are at first evident at the outside limits of the phloem, but these are soon crushed by the enlargement of cells which differentiate as sieve tubes and companion cells. The primary xylem is differentiated centripetally. The protoxylem elements have annular-spiral thickenings, and the metaxylem scalariform thickenings.

PROVASCULAR SEEDLING ANATOMY

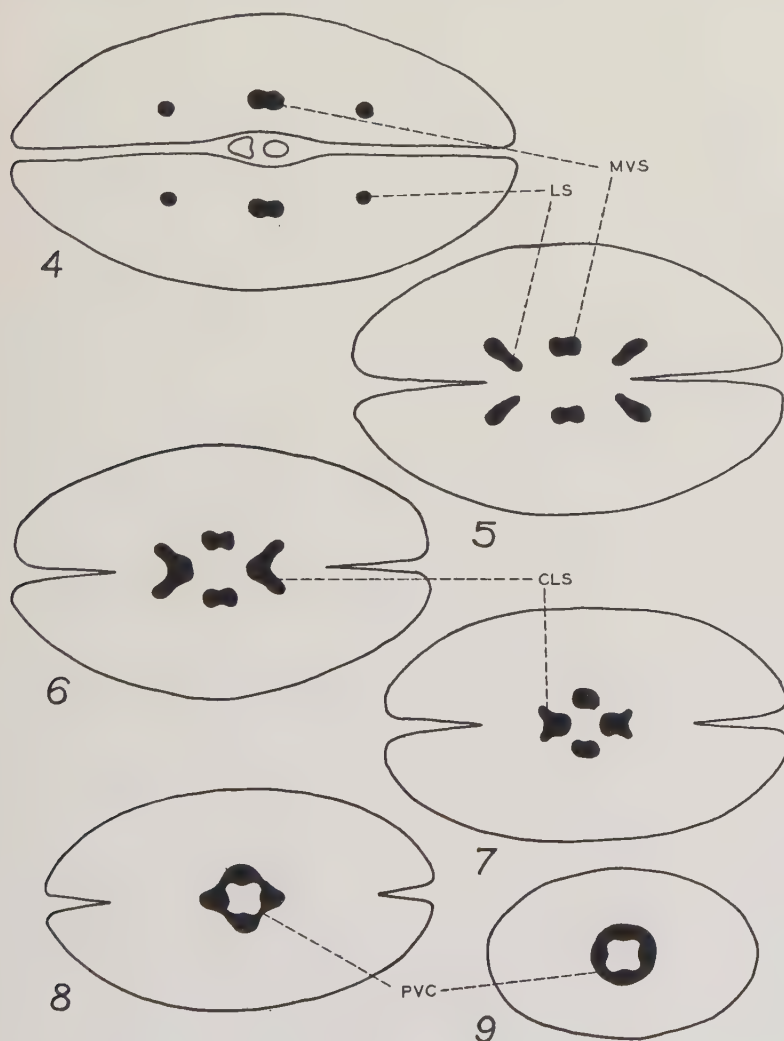
In a day-old seedling the provascular strands can easily be traced and the ultimate arrangement of the vascular system is clearly indicated.

In each cotyledon there is a median strand of provascular tissue flanked on either side by one or more smaller lateral strands (fig. 4). The number of laterals in the cotyledons varies, one or two being the usual number, although some cotyledons have been observed with one lateral strand on one side of the midvein and two on the other. In cross section the provascular strand of the midvein appears lobed, while the lateral strands are circular. The cells of the mesophyll region of the cotyledon are filled with large inulin sphaerocrystals, which take a deep stain, while the cells of the provascular strands are not so large and are not filled with these large crystals but contain a minutely granular substance which does not stain deeply.

At this age the phloem and xylem regions are not differentiated, but a little later in the ontogeny primary phloem ducts are differentiated, and concurrently with the formation of these ducts the first annular protoxylem elements are matured. The initial differentiation of vascular tissue occurs near the base of the cotyledonary petiole and proceeds both upward and downward. This development differs from that of the root in that the protoxylem of the root does not differentiate until after the primary phloem is well defined.

In tracing the provascular strands downward from the cotyledons through the hypocotyl to the meristematic region of the root, they remain separate to a level just below the point of divergence of the cotyledons. At this level the lateral strands occupy a more central position (fig. 5), and still lower in the hypocotyledonary axis the lateral strands from opposite cotyledons converge (fig. 6). This results in the formation of two strands in the cotyledonary plane on opposite sides of the axis of the hypocotyl (fig. 7). When there are two lateral strands on each side of the midvein, the outermost strands of each cotyledon converge to form a common strand, with their counterpart in the opposed cotyledon, and these in turn anastomose with the common strand of the inner laterals of each cotyledon (fig. 22).

The midvein strands, which appear lobed in cross section in the cotyledons (figs. 4-6), become ovate in outline near the base of the cotyledons (fig. 7). The two median strands then converge in the hypocotyl with the united lateral strands to form the fluted central



FIGS. 4-9.—Cross sections through young embryo. Provascular strands shown in black. *cls*, united lateral strand of opposite cotyledons; *ls*, lateral strand; *mvs*, midvein strand; *pvc*, provascular cylinder.

provascular cylinder (fig. 8). The lobed condition of this cylinder is less evident at lower levels (fig. 9) and the stele becomes circular in cross section. This cylinder of cells has at its center larger cells (fig. 2) whose cytoplasmic contents are less dense than those surrounding them.

VASCULAR ANATOMY OF HYPOCOTYL AND COTYLEDONS

The course of the vascular bundles of the cotyledons and hypocotyl is shown graphically (fig. 22). In the following description the bundles are traced from their point of initiation in the cotyledons to the diarch root. To avoid confusion, the median bundle is first discussed and then the course of the lateral bundles of the cotyledons is considered.

About midway between the base and the tip of the cotyledon of a three- to ten-day old seedling, there have been differentiated two vascular bundles which constitute the midvein. The two protoxylem strands of each bundle lie in close association with each other and the metaxylem is tangentially oriented with respect to the protoxylem (fig. 16). The phloem of each bundle lies in an abaxial position in relation to each metaxylem group. These two closely associated bundles are surrounded by a sclerenchymatous sheath of cells whose walls are distinctly thicker than those of the mesophyll cells.

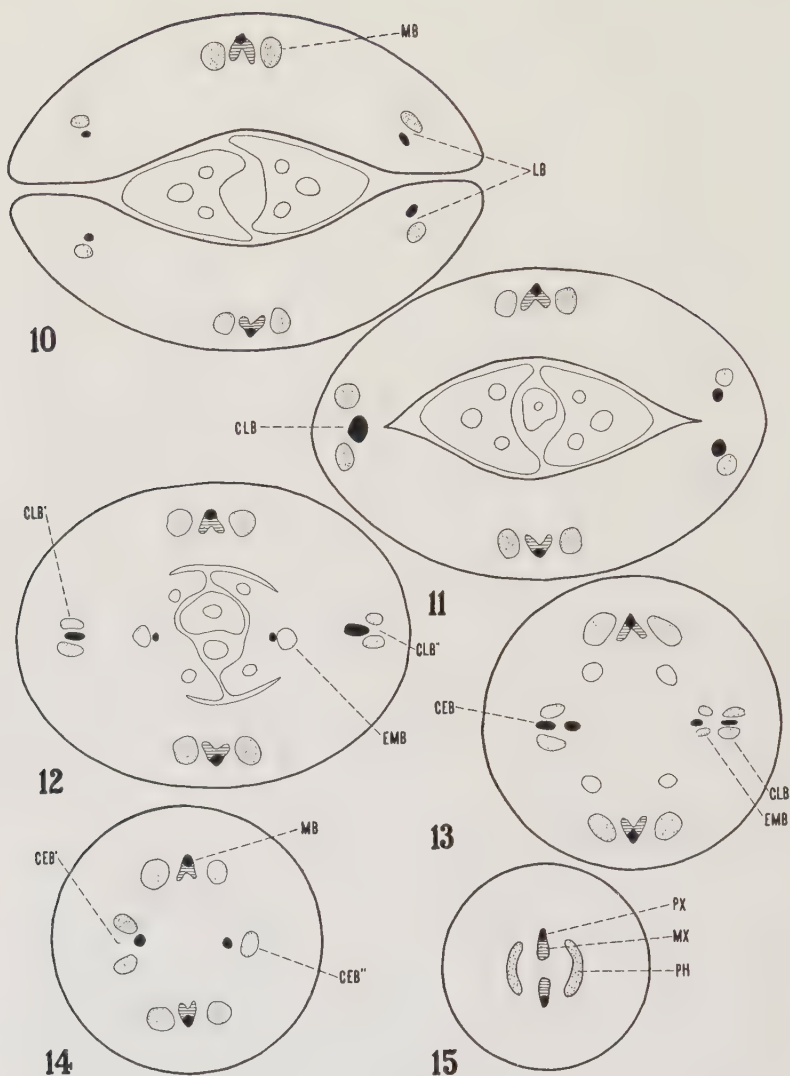
THOMAS (16, 17) discusses the double bundle, which sometimes constitutes the midvein of the cotyledons, in relation to types of transition found in certain seedlings. The double bundle is reported as consisting of two groups of primary phloem with a single strand of protoxylem between, the three groups being in radial arrangement; but no mention is made of the metaxylem of this bundle. In *Cynara scolymus* the metaxylem is very evident and the midvein is truly a double bundle located along the median line of the cotyledon and consisting of two separate strands, each of which contains protoxylem, metaxylem, and phloem. The vascular elements of these two distinct bundles, however, are inclosed in a common sheath (fig. 16). The two protoxylem strands unite near the base of the cotyledon, in the petiole, so that the bundle contains two groups of phloem, two groups of metaxylem, but only one common protoxylem group. At a lower level, at the base of the hypocotyl, the metaxylem

groups also unite, but the two phloem strands of each double bundle never unite to form a common strand. Instead one phloem strand on each side of the median bundle of one cotyledon unites with the equivalent phloem strand of the opposed cotyledonary median bundle to form the lateral phloem strands of the diarch root. The interpretation of the median bundle as a double one depends, therefore, upon the level at which sections are taken.

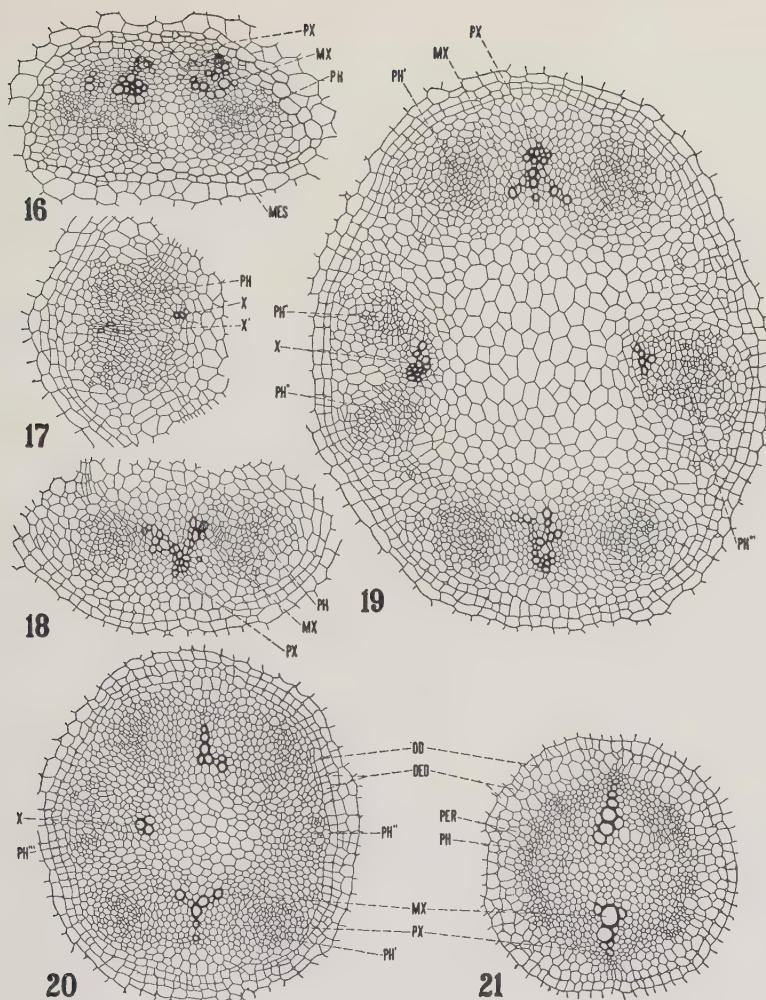
At the base of each cotyledon and below the point where the protoxylem strands of the double bundle have converged, there is formed a bundle which has the primary xylem in a V-shaped arrangement. The protoxylem lies in an abaxial position at the apex of the V and the two metaxylem groups form the arms. The strands of primary phloem lie on either side of the metaxylem (fig. 10mb). This arrangement of the median bundle is also found in the upper part of the hypocotyl (fig. 18). At successively lower levels (figs. 19, 20) in the hypocotyl the differentiation of metaxylem with reference to the protoxylem is more and more centripetal, which brings the two arms of metaxylem into closer association. The two strands of phloem still lie in a lateral position with reference to the primary xylem (fig. 14mb). At the base of the hypocotyl the primary xylem differentiates in the exarch manner of the root (fig. 21), and the two groups of phloem on each side of the intercotyledonary plane converge, forming a single strand of phloem on either side of the primary xylem (figs. 15, 21).

The lateral bundles of the cotyledons are endarch collateral (fig. 10lb), but at a level just below the divergence of the cotyledons they converge toward the cotyledonary plane, and the xylem of the lateral bundles of opposite cotyledons unites (fig. 11clb). This fusion bundle then consists of xylem flanked on either side, parallel to the intercotyledonary plane, by phloem (fig. 12clb'). The phloem becomes reoriented at a lower level (figs. 12clb'', 14ceb') and finally lies outside of the xylem and on the same radius (fig. 14ceb''). Ultimately this vascular unit ends blindly in the lower hypocotyl (fig. 20).

LEE (7) and SILER (12) both describe transitions very similar to that described here for *Cynara scolymus*. LEE discusses the transition of *Arctium majus*, while SILER discusses a like transition for *A. minus*. The main facts of the transition in these two species con-



FIGS. 10-15.—Diagrammatic representation of vascular anatomy of three- to ten-day old seedling. Primary xylem shown by black; metaxylem, lined; primary phloem, stippled. *ceb*, bundle composed of midvein of epicotyledonary leaf and combined lateral veins of opposed cotyledons; *clb*, combined lateral bundle of opposite cotyledons; *emb*, midvein of epicotyledonary leaf; *lb*, lateral bundles of cotyledons; *mb*, median bundle; *mx*, metaxylem of root; *ph*, primary phloem; *px*, protoxylem of root.



FIGS. 16-21.—Cellular details of transition and root: Fig. 16, structure of double bundle of midvein of cotyledon. *ph*, phloem; *px*, protoxylem; *mes*, mesophyll; *mx*, metaxylem. Fig. 17, epicotyledonary bundle converging with lateral cotyledonary bundle. *ph*, phloem of both bundles united; *x*, xylem of epicotyledonary leaf; *x'*, of lateral cotyledonary bundle. Fig. 18, cotyledonary midvein bundle in upper part of hypocotyl. Fig. 19, middle of hypocotyl. *ph'*, phloem of bundle in cotyledonary plane; *ph''*, in intercotyledonary plane; *x*, xylem of intercotyledonary bundle; *ph'''*, phloem of intercotyledonary bundles united. Figs. 20, 21, section at base of hypocotyl and root respectively. *ded*, double endodermis; *od*, oil ducts; *per*, pericycle; *ph*, phloem of root; *ph'*, of bundle in cotyledonary plane; *ph''*, in intercotyledonary plane (xylem has not differentiated); *ph'''*, phloem of opposite bundle; *x*, xylem of bundle in intercotyledonary plane.

form to those found in *C. scolymus*. The merging of the lateral cotyledonary bundles with the metaxylem of the cotyledonary midvein bundle which they describe for these species is not encountered in *C. scolymus*. Instead in the young seedlings these lateral bundles end

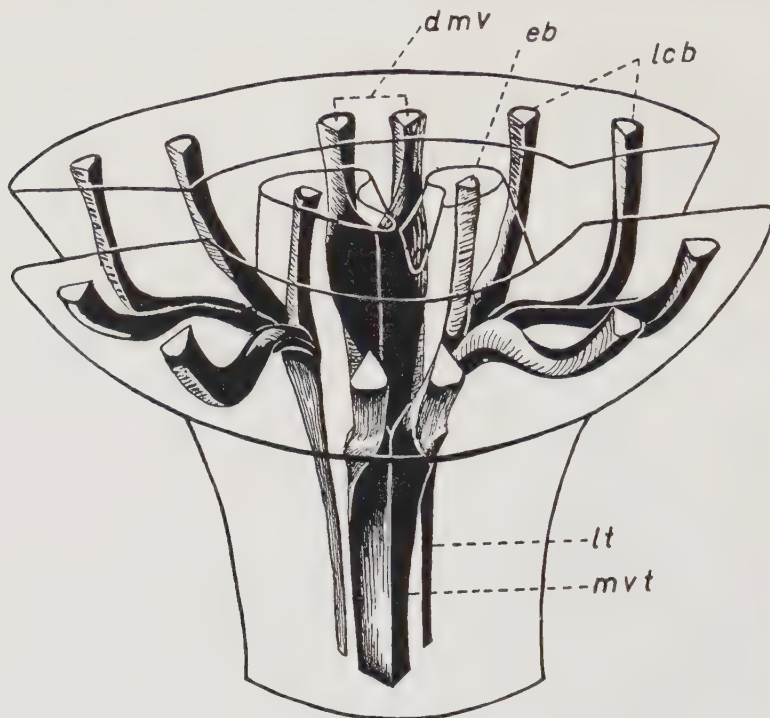


FIG. 22.—Schematic diagram of seedling vascular system showing two laterals on each side of midvein bundle. *eb*, epicotyledonary midvein bundle; *lcb*, lateral cotyledonary bundle; *lt*, lateral bundle of intercotyledonary plane; *mvt*, bundle of cotyledonary plane; *dmv*, double midvein bundle.

blindly in the hypocotyl. The only connection between these lateral bundles and the primary vascular elements of the root is by means of secondary tissues which are laid down by the cambium later in the ontogeny of the axis.

VASCULAR SYSTEM OF EPICOTYL

In a three- to ten-day old seedling the first two foliar leaves have developed provascular tissue consisting of a median bundle with a

lateral bundle on either side. At about the level of divergence of the cotyledons, the median bundle of the epicotyledonary leaf has differentiated as a collateral endarch bundle consisting of protoxylem and phloem (fig. 12emb). At a slightly lower level the phloem differentiates as two strands, which come to lie on either side of the xylem in a plane parallel to the cotyledonary plane (fig. 13emb). This midvein trace extends downward, and at about the middle of the hypocotyl unites with the cotyledonary trace, which lies in the intercotyledonary plane. The phloem strands of the combining bundles unite at a higher level (figs. 13ceb, 17) than do the xylem strands. After the xylem of the two bundles unites, the combined bundle consists of xylem flanked on either side by phloem. Near the base of the hypocotyl this bundle forms a collateral bundle by the convergence of the phloem strands (fig. 14ceb', ceb'').

Summary

1. Germination of the seed and development of the seedling of *Cynara scolymus* are discussed.

2. The embryo shows well defined provascular strands which later differentiate vascular tissue.

3. The primary root is diarch with three clearly defined histogens. The plerome and periblem give rise to the stele and cortex respectively, while the root cap and epidermis are derived from a common histogen, the calyptogen-dermatogen.

4. The order of differentiation of the primary vascular elements is described.

5. The primary endodermal oil ducts arise schizogenously between the layers of the double endodermis.

6. In the transition, the primary xylem of the root in the cotyledonary plane is continuous with the xylem of the midveins of the cotyledons. The lateral bundles of the cotyledons end blindly in the intercotyledonary plane of the hypocotyl.

7. The structure of the double bundle of the cotyledon is described.

8. The midveins of the first foliar leaves anastomose with the lateral bundles of the cotyledons in the hypocotyl.

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